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The Reproductive Cycle of the Trochid Gastropod *Oxystele variegata* (Anton, 1839)

by

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Abstract. *Oxystele variegata* (Anton, 1839) is a trochid gastropod found commonly in the southern African intertidal region. Monthly samples over a one-year period were examined for gonadal development by comparing dry somatic and gonadal tissue weights and histological sections. Mature oocytes and sperm could be found in monthly samples of the gonads of all animals over 10 mm in size throughout the year, but based on changes in gonadal weights two spawning peaks were detected—one in February and a second in September to October. It seems likely that this temperate species is able to spawn throughout the year but that spawning is intensified during these peak periods.

INTRODUCTION

Oxystele variegata (Anton, 1839) is a trochid gastropod which occurs commonly in the rocky intertidal zone in estuaries and along the southern African coast from southern Angola (KENSLEY & PENRITH, 1972) to Durban in South Africa (DAY, 1974). It is one of four species in the genus *Oxystele* that are found in the balanoid zone, where it is very prominent. Because of its abundance *O. variegata* must be a major contributor to the energy budget of this zone. Based on measurements of the metabolic rate of this species, KING (1974) estimated that the annual population production was 46.4 $kJ \cdot m^{-2} \cdot yr^{-1}$. MCQUAID (1980, 1982a) has described how the population of *O. variegata* is zoned according to size with the largest animals in the upper balanoid zone and the smallest lower on the shore. No attempt has yet been made to ascertain the breeding cycle with any certainty, but MCQUAID (1980) hypothesized from settlement patterns that spawning occurred throughout the year, with a peak in February and two smaller peaks in May/June and September/October, 1977.

Monodonta lineata, a related trochid of the northern cool temperate regions, has been investigated by DESAI (1966), who found that this species spawned from May to August with male and female gonads showing similar cycles. UNDERWOOD (1972) investigated the breeding cycle of the British trochids *M. lineata, Gibbula umbilicalis,* and *G. cineraria.* He found that *M. lineata* and *G. umbilicalis* spawned throughout July and August and less in September. However, *G. cineraria* did not provide clear evidence of spawning since histological sections of the gonads appeared the same throughout the year.

UNDERWOOD (1974) also found that the trochid *Austrocochlea constricta,* which occurs on the west and southwest coast of Australia, did not show any seasonal change in the appearance or histology of the gonad, and he concluded that this species spawned throughout the year with a peak in October/November. PAINE (1971), using energy content as a measure of reproductive state, concluded that the western North American trochid *Tegula funebralis* spawned once a year during the summer.

In this paper a description is given of the breeding cycle of *Oxystele variegata,* based on changes in the ratio of gonadal/somatic dry weight and gonadal histology during the course of a full year.

MATERIAL AND METHODS

Monthly samples of *Oxystele variegata* were collected at random from the upper balanoid zone at Dalebrook on the Cape Peninsula (47°07′S, 18°27′E) during the period April, 1980, to March, 1981. The animals were preserved in a 5% formalin solution until they could be examined.

Fifteen to 20 animals of each sex were dissected each month. Every shell was measured across the base at the widest point and the animal was then removed and the operculum cut off and measured. The gonad was dissected out of the somatic tissue and both gonadal and somatic tissue were dried in an oven at 55°C for 24 h. The dry

Table 1

Mean monthly shell sizes and opercular diameters of *Oxystele variegata* sampled for gonadal development.

Month	Shell size (mm) ♂	Shell size (mm) ♀	Opercular diameter (mm) ♂	Opercular diameter (mm) ♀
April, 1980	14.9	14.8	5.4	5.5
May	16.4	16.0	6.0	5.8
June	16.0	16.0	5.8	5.6
August	15.5	16.2	5.4	5.3
September	16.8	16.7	6.0	6.0
October	16.6	16.5	6.0	5.9
November	16.8	16.4	5.8	5.8
December	15.6	16.0	6.1	5.9
January, 1981	15.6	15.5	5.6	5.8
February	16.5	16.5	5.9	5.9
March	15.3	16.5	5.4	6.0
Annual mean	16.0	16.1	5.8	5.8

weights of the gonad and of the somatic tissue for each animal were measured.

In addition to the above animals, two to five specimens of each sex were collected each month and used to obtain histological sections of the gonads. The gonads of these preserved specimens were dehydrated in alcohol and blocked in paraffin wax. Transverse sections were cut through the center of the gonads at 10 μm. The sections were dehydrated in alcohol and stained with hematoxylin and eosin.

The male and female gonadal weights were linearly regressed on somatic tissue weights for each month. The data obtained from these regressions were used to calculate monthly gonadal indices. These indices were defined as the ratio of gonadal to somatic weight, expressed as a percentage for a standard animal of 0.07 g somatic weight (with an opercular diameter averaging 5.8 mm).

RESULTS

All specimens dissected, ranging from 13.6 mm to 21.6 mm shell width, had mature gonads throughout the sampling period. Individuals of *Oxystele variegata* less than 10.0 mm shell width lacked gonads and progressively larger gonads could be found in animals with a shell width of 10.0 mm and upwards.

In both males and females of *O. variegata* the gonads lie adjacent to and above the digestive gland, extending into the shell spiral up to the apex. As with most archaeogastropods, trochids release the unfertilized gametes directly to the surrounding environment where fertilization occurs (Fretter & Graham, 1962; Desai, 1966; Paine, 1971; Underwood, 1972; Branch, 1974). *Oxystele variegata* probably conforms to this pattern since we observed no egg laying or egg masses. The male gonad is a pinkish, densely constituted tissue. Histological sections showed that

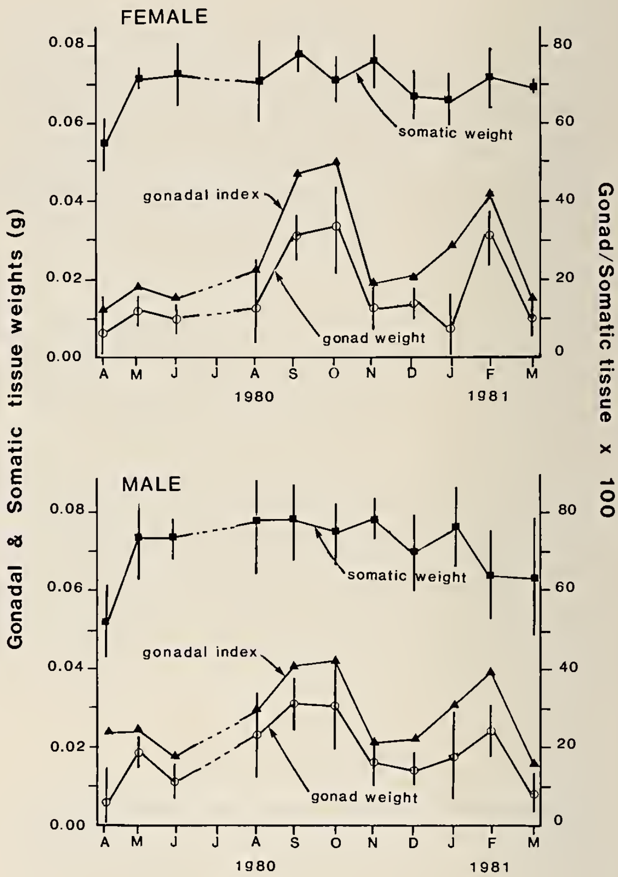

Figure 1

Gonadal and somatic dry tissue weights (g) of "standard" *Oxystele variegata* with an opercular diameter of 5.8 mm and the gonadal index (expressed as a ratio of gonad : somatic weight × 100) plotted against time (month). (Bars indicate 95% confidence levels.)

there were ripe spermatozoa present throughout the year. The ratio of spermatozoa to spermatids and spermatocytes differed from individual to individual in the same month, but spermatozoa never constituted less than 50% of the area of the testis (as determined from grid counts of the gonadal sections). The female gonad contains a mass of white or creamy oocytes, each within a clear jelly coat which is a feature of the trochids (Fretter & Graham, 1962; Desai, 1966; Duch, 1969; Underwood, 1972, 1974; Simpson, 1977; Webber, 1977; Heslinga, 1981). Mature oocytes were present throughout the year and had an average diameter of 180 μm, not including the jelly coat. Histological sections showed immature oocytes were also present throughout the year, but not common from January to February or from August to September. No difference existed in mean shell or opercular diameters between the sexes of the animals sampled (Table 1).

The gonadal indices show strong correlation between the sexes, both peaking from September to October, 1980, and in February, 1981, and both dropping in November, 1980, and March, 1981 (Figure 1). Since this gonadal index can be affected by changes in somatic weight, an independent assessment of changes in somatic and gonadal weights was also undertaken. Both gonadal and somatic weights were linearly regressed on opercular diameter for each month. These regressions are shown in Table 2. From these regressions the gonadal and somatic weights of animals with a standard opercular diameter of 5.8 mm could be calculated for each month. The somatic weights fluctuated about a mean of 0.07 g for each sex. As shown in Figure 1 the somatic weights of both sexes peaked above the mean in September and November and dropped below the mean in April. The gonadal weights of both sexes reflected the gonadal indices almost completely, thus confirming that in spite of slight changes in the somatic weight the gonadal index is a reliable measure of reproductive activity.

The number of non-significant correlations between gonadal weight and opercular diameter seen in Table 2 indicates a wide "scatter" amongst the population in certain months, particularly the males. This scatter is due to the fact that some individuals are sexually mature at a time when others have just spawned. Again, however, there was a strong correlation between the sexes for both the gonadal and somatic tissue weights, and we are confident that the gonadal index and changes of gonadal weights do reflect reproductive cycles.

DISCUSSION

It appears that *Oxystele variegata,* as with some other trochids (Underwood, 1972, 1974; Simpson, 1977) exhibits continuous gametogenesis once mature. Synchronization of spawning still remains important since fertilization is external and, indeed, the male and female gonadal weights do peak and fall in unison (Figure 1). *Oxystele variegata* congregates in large numbers in the upper balanoid zone at Dalebrook thus also ensuring proximity of the sexes during spawning. Desai (1966), Duch (1969), and Simpson (1977) also found this clustering behavior in trochids.

Despite this, the gonadal tissue weights (relative to opercular diameter) showed marked variation between individuals, particularly around the periods of peak spawning. However, in all samples dissected during other months there were always some specimens whose gonadal weights were well above or below the average and these were considered to be in pre- or postspawn states respectively. Such variation in the gonadal weights within the population probably indicates that there are some individuals that spawn out of phase with the bulk of the population. The presence of some spawned individuals in virtually every month of the year suggests that spawning occurs year round although peaking twice a year. These variations in gonadal weight are reflected in the number of months in which there were non-significant correlations between gonadal weights and opercular diameter (Table 2), in contrast to the generally high correlations between somatic tissue weight and opercular diameter. The two main gonadal peaks indicate spring and late summer spawnings with the build up to the spring spawning (September to October) being more prolonged. At present we have no evidence whether these peaks repeat each year.

It is also apparent from the histological sections, which showed a constant supply of ripe ova and sperm in the gonads, and from the irregular but continuous settlement of recruits to the low shore (McQuaid, 1982b), that spawning probably occurs throughout the year, peaking in the spring and late summer.

The somatic tissue weights of standard-sized animals of both sexes remained steady at a mean of 0.07 g, except for April when they declined. This fall in somatic weight is possibly because during this period there is a recruitment of new individuals to this zone (McQuaid, 1982b) and we speculate that increased feeding competition may strain existing food sources. By May to June the population has declined due to mortality and the somatic weight increases (Figure 1) together with new algal growth in autumn. In the upper balanoid zone, from where our samples were taken, there are only two main macroalgae—*Porphyra capensis* and *Gelidium pristoides.* McQuaid (1980) found that both these species have varied calorific values during the year. *Porphyra capensis* declined in calorific value during autumn whilst *G. pristoides* had a maximum value in autumn. The drop in calorific value of some of the food available for *Oxystele variegata* could affect the somatic weights, but we found that *O. variegata* were not commonly seen on macroalgae, and they possibly mainly feed on microalgae and sporelings rasped from the substratum. This is also the opinion of McQuaid (1982a). A drop in the number of sporelings has been found during April in an analysis of monthly colonization carried out by Joska (in preparation) and this, too, could explain the lower somatic weight during this month.

In archaeogastropods the larval stage is brief (Fretter & Graham, 1962; Desai, 1966; Underwood, 1972; Webber, 1977) and settlement on the shore should take place within a week of spawning. McQuaid (1982a, b) found that 5 to 6-mm specimens of *O. variegata* were detectable in large numbers in February with a smaller peak in June/July. In addition, small numbers could be found throughout the year. Since specimens of *O. variegata* take about four months to reach a size of 5 to 6 mm, these juveniles probably settled about four months earlier, and are likely to have been the result of, respectively, the spring and late summer spawnings that we have recorded.

Temperature is a factor often cited as being of great importance for spawning or reproduction in marine invertebrates. During the period of sampling the sea temperatures rose during the spring spawning but fell at the time of the late summer spawning (Figure 2). Apart from suggesting that a minimum temperature exists for spawning, there is no obvious influence of temperature on the

Table 2

Regression coefficients for regressions of gonad weight (y) on operculum diameter (x): $y = a_0 + a_1x$ and coefficients of determination (r^2) with the probability that r^2 is significant (P).

	Month	a_0	a_1	r^2	P
♀	April, 1980	−0.0155	0.0382	0.2729	0.05
	May	−0.0340	0.0794	0.4638	0.001
	June	−0.0152	0.0436	0.2915	0.05
	August	0.0194	−0.0046	0.0026	Not significant
	September	−0.0290	0.1103	0.2988	0.01
	October	−0.0034	0.0630	0.0232	Not significant
	November	−0.0252	0.0672	0.3400	0.01
	December	−0.0093	0.0399	0.2495	0.05
	January, 1981	0.0058	0.0251	0.0214	Not significant
	February	−0.0676	0.1691	0.5365	0.001
	March	−0.0281	0.0666	0.5426	0.001
♂	April, 1980	−0.0222	0.0531	0.1509	Not significant
	May	0.0374	−0.0317	0.0228	Not significant
	June	−0.0661	0.1363	0.5817	0.001
	August	−0.0017	0.0439	0.1618	Not significant
	September	−0.0310	0.1093	0.1910	0.05
	October	−0.0195	0.0870	0.1710	0.05
	November	−0.0152	0.0535	0.4046	0.01
	December	0.0020	0.0231	0.1047	Not significant
	January, 1981	−0.0239	0.0707	0.1925	0.05
	February	−0.0820	0.1823	0.6314	0.01
	March	−0.0156	0.0433	0.0940	Not significant

Regression coefficients for regressions of somatic tissue weight (y) on operculum diameter (x): $y = a_0 + a_1x$ and coefficients of determination (r^2) with the probability that r^2 is significant (P).

	Month	a_0	a_1	r^2	P
♀	April, 1980	0.0346	0.0317	0.9934	0.001
	May	−0.1638	0.4054	0.8411	0.001
	June	−0.0601	0.2269	0.4540	0.01
	August	0.0622	0.0144	0.0049	Not significant
	September	−0.0863	0.2825	0.7607	0.001
	October	−0.1844	0.4410	0.7384	0.001
	November	−0.0926	0.2923	0.5173	0.001
	December	−0.0940	0.2788	0.4958	0.001
	January, 1981	−0.1105	0.3049	0.7235	0.001
	February	−0.1199	0.3335	0.5736	0.001
	March	−0.1688	0.4166	0.8663	0.001
♂	April, 1980	−0.0229	0.1282	0.4085	0.01
	May	−0.0199	0.1610	0.2331	0.05
	June	−0.1480	0.3823	0.5455	0.001
	August	0.0370	0.0659	0.1417	Not significant
	September	−0.1046	0.3129	0.6867	0.001
	October	−0.1327	0.3571	0.8634	0.001
	November	−0.0941	0.2979	0.6955	0.001
	December	−0.0296	0.1709	0.5703	0.001
	January, 1981	−0.0758	0.2295	0.6760	0.001
	February	−0.1319	0.3389	0.8117	0.001
	March	−0.1237	0.3222	0.5280	0.001

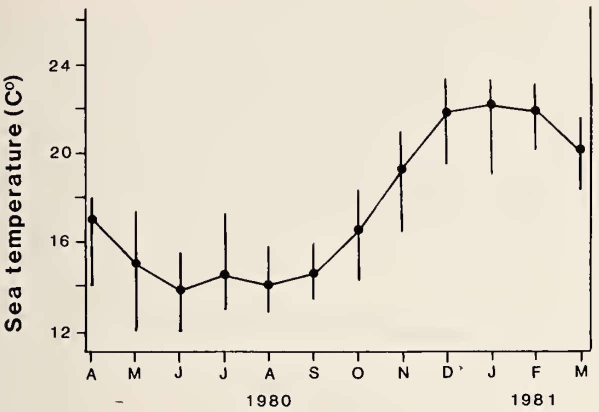

Figure 2

Mean monthly sea temperatures during the sampling period. Bars indicate maximum and minimum temperatures. (Temperature records kindly supplied by the Department of Maritime Defence, Simonstown.)

reproductive cycle in this species. Dalebrook lies in False Bay, which because of its shallow waters and current patterns affords year round moderate conditions and predictable seasonal changes in temperature. Rather more variant conditions on the west coast could possibly produce different spawning peaks.

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